

## Opinion

### A Rebuttal to the Arnold Classification of *Speyeria callippe* (Nymphalidae) and Defense of the Subspecies Concept

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**Abstract.** In a provocative paper (Pan-Pacific Entomologist 61:1-23), Richard A. Arnold has proposed that the taxonomic classification of subspecies within *Speyeria callippe* (Boisduval) should be essentially eliminated for three different reasons. These include (1) most subspecies are heterogeneous with much clinal intergradation, (2) most independent characters vary discordantly, and (3) most diagnostic characters are only "minor" or "slight" differences in wing color pattern. If these views are applied to the entire genus, the taxonomic classification of *Speyeria* below the species level would be nearly abolished. The present paper reviews and rebuts the methodology and conclusions presented in the Arnold study. The general philosophy of the subspecies concept is discussed with respect to *Speyeria*. It is argued that the differences between *Speyeria* subspecies are often far greater than between full species, and that the three criticisms of the subspecies concept presented by Arnold equally apply to most full species of *Speyeria*. Finally, it is also argued that *Speyeria* subspecies represent tangible and significant units of evolutionary divergence, and that the historical classification of *Speyeria* subspecies is fully warranted and should be retained.

The nymphalid butterfly genus *Speyeria* is well known for the tremendous diversity of geographic variation in wing phenotype evident throughout most of the group. This variation was once recognized by the taxonomic classification of over 100 typological "species" within the genus. Later, dos Passos and Grey (1947) found evidence of extensive clinal intergradation among many of these "species", therefore reducing these taxa to subspecies status. As a result of their study, the diversity observed within *Speyeria* was reclassified into 13 biological species.

Recently, Arnold (1985) has conducted a complex statistical study of the geographic variation found in one of these species groups, *Speyeria callippe* (Boisduval). On the basis of this work, Arnold concluded that most of the geographic variation perceived within *S. callippe* is not statistically significant, and that the taxonomic classification of subspecies should be essentially abolished. Moreover, the geographic variation seen

in *S. callippe* is quite typical of the genus as a whole. If this approach and philosophy were applied to the entire genus, the taxonomic classification of *Speyeria* below the species level would be virtually eliminated.

However, Arnold's study is subject to vigorous challenge regarding the accuracy and validity of both its methodology and data. In addition, the more basic philosophy expressed in this paper regarding the subspecies concept and taxonomic classification is also subject to strong debate. Both of these issues will be addressed in this review of the Arnold study.

Many errors and deficiencies are evident in the data and methodology employed by Arnold in his study. He has used the statistical techniques of variance analysis, principal components analysis, and discriminant function analysis to examine geographic patterns in eight different wing characters. The first error lies in his choice of characters used for analysis, which include five wing dimension characters and three color pattern characters. Contrary to Arnold's statement on page 4 of his paper, wing size has never been regarded as a particularly significant component of the geographic variation within *Speyeria callippe* or in the taxonomic delineation of subspecies. Wing length is only of significance when comparing geographically contiguous populations or subspecies, for example San Francisco *S. c. callippe* and inland *S. c. comstocki*. Characters of wing pattern and color are the primary factors involved in the geographic variation of this species as outlined in an earlier paper (Arnold, 1983). As a consequence, five of the eight characters used by Arnold in his analysis are essentially irrelevant to the larger patterns of geographic variation within *S. callippe* and should have been excluded from the study.

Thus, only three characters of wing color pattern that do exhibit significant geographic variation, were used in the study including dorsal ground color, ventral disc color, and ventral spot silvering. However, there are serious flaws in Arnold's analysis of these characters as well. Moreover, it appears that Arnold has substantial errors in his taxonomic concepts of *S. callippe* subspecies as shown in his page 2 map. These errors are outlined as follows:

1. Arnold placed *S. c. meadii* in northwestern Colorado. However, this subspecies is limited to the Colorado Front Ranges east of the Continental Divide. Populations in western Colorado are closer to subspecies *S. c. harmonia*.

2. Arnold placed *S. c. nevadensis* across Nevada, but placed *S. c. laura* east of Lake Tahoe. In fact, the subspecies *S. c. nevadensis* is limited to the Sierra Nevada east slope in eastern California and western Nevada. Populations in central and eastern Nevada belong to subspecies *S. c. harmonia*. The name "*laura*" is not known to represent any discrete population, but was applied to an extreme individual in Sierran *S. c. nevadensis* populations near Lake Tahoe.

3. Arnold largely ignored the important geographic variation in *S. callippe* across the Sierra Nevada, perhaps because of the considerable taxonomic confusion that currently surrounds this variation. The unsilvered populations at low elevations along the west slope of the Sierra Nevada are properly called *S. c. inornata* rather than *S. c. juba* as denoted by Arnold. Both taxa were originally described from Downieville, Sierra County, although this type locality is not particularly appropriate for either taxon. Relatively uniform or "pure" populations of *S. c. inornata* are actually restricted to the low foothills extending from northern Tulare County north to Shasta County. Although the name "*inornata*" may pose a nomenclatural problem, these populations comprise a very distinctive subspecies that certainly warrants recognition.

4. The names *juba* and *sierra* apply to silvered populations at high elevations that intergrade between *S. c. inornata* and *S. c. nevadensis* along a sharp east-west stepcline. Populations found on the west slope (i.e. Quincy-Downieville region) resemble the lectotype of *S. c. laura*, but the designated type locality of *laura* at Carson City, Nevada, is not appropriate. The populations on the east slope (i.e. Mt. Ingalls-Gold Lake region) have been named *S. c. sierra* dos Passos and Grey. However, L. Paul Grey (pers. comm.) has recently examined the lectotype of *S. c. juba*, and found that it matches the phenotype of the east slope subspecies. Thus, the name *sierra* must be regarded as a synonym of *S. c. juba*, and the actual type locality is probably closer to Gold Lake rather than Downieville.

5. Arnold has transposed the names *laurina* and *macaria* on his page 2 map, since *S. c. macaria* occupies the Tehachapi Mountains while *S. c. laurina* occurs on the west slope of the Greenhorn Mountains. Presumably the samples shown in his Table 1 are correctly identified.

Detailed descriptions of the *S. callippe* subspecies together with their distributions are outlined in Appendix I.

A third major flaw in Arnold's analysis is the failure of his methodology in detecting significant geographic variation in dorsal wing color as outlined by Hovanitz (1943). A particularly dramatic example of this is the comparison of the San Francisco *S. callippe callippe* with *S. c. liliana* of Napa and Lake Counties. The typical *S. c. callippe* subspecies is one of the most divergent and distinctive taxa within the species. It is characterized by pale yellow-orange ground color combined with extremely intense melanic suffusion on the dorsal wing surfaces. In addition, the subspecies exhibits a dark to medium brown disc covered with extensive yellow overscaling on the ventral hindwing. By sharp contrast, *S. c. liliana* exhibits a darker reddish orange ground color on the dorsal surfaces combined with reduced melanic basal suffusion. Furthermore, *S. c. liliana* exhibits a solid, dark red-brown disc with little or no evidence of yellow overscaling. I have examined several hundred specimens of both *S.*



*c. callippe* and *S. c. liliana*, and these differences are nearly constant at a frequency greater than 90%. Yet Arnold completely fails to resolve this extreme divergence in his own analysis outlined in his Figure 7. The only *S. callippe* subspecies that even remotely resembles the typical subspecies are the *S. c. comstocki* populations of the central-southern Coast Range, and these are consistently paler in color with reduced melanic suffusion compared to the San Francisco populations (see below). It is not clear why Arnold's methodology has failed in the analysis of dorsal coloration, but perception problems in the scoring of the raw data are a possibility.

A fourth error is seen in the analysis of spot silvering on the ventral hindwing, which may be due to faulty data. The unsilvered form is largely restricted to low elevations along the west slope of the Sierra Nevada and in the Salmon-Siskiyou Mountains of northern California. This trait is very rare or completely absent in populations along the east slope of the Sierra Nevada. Yet Arnold depicts a very high frequency of unsilvering east of Lake Tahoe in his Figure 8, which is certainly not seen in the *S. callippe nevadensis* populations of that region. I would suspect that his sample of *S. c. "laura"* specimens may have faulty locality data.

A fifth error is seen in the analysis of ventral disc color, which undoubtedly reflects inadequate sampling and geographic coverage. In his Figure 9, Arnold suggests that there is a sharp geographic discontinuity between the green and brown disc forms with very little overlap in populations. This is simply not true. In fact, the green form dominates in populations along the east slope of the Sierra Nevada from Inyo County north to Lassen County, and there is extensive mixing of the green and brown forms together with intermediates in populations extending from Eldorado County north to Klamath County, Oregon. Moreover, the *S. c. semivirida* populations are also extremely heterogeneous in disc color, with green, brown, and intermediate color forms occurring together throughout the populations extending from southern Oregon to British Columbia and east to western Idaho. Therefore, since extensive mixing of disc colors does in fact occur within populations over wide geographical areas, disc color can not be used as a single diagnostic character to distinguish subspecies. Hence in accordance with Arnold's philosophy, virtually no taxonomic subspecies within *S. callippe* should be recognized!

However, this philosophy concerning the subspecies concept and its taxonomy requires close scrutiny. The questions raised by Arnold in his treatment of *Speyeria callippe* received a long and extensive debate several decades ago, and Pimentel (1959) has provided a good review of this debate. Certainly these questions have direct relevance to the taxonomic classification of *Speyeria*.

Geographic subspecies exhibit the following characteristics when



strong isolating barriers are either presently absent or were absent in the relatively recent past (i.e. 15,000 years ago):

1. Subspecies exhibit clinal intergradation with other subspecies in geographically contiguous regions.

2. Subspecies rarely exhibit complete homogeneity for any single character, and most characters are shared by more than one subspecies.

3. Independent characters usually exhibit discordant geographic variation.

4. As a consequence of the above, most subspecies are defined by a particular combination of characters which occur at a reasonably high frequency within the populations of the subspecies.

The absence of these features when no geographic barriers are present suggests reproductive isolation and full species status. Therefore, these characteristics serve to distinguish the subspecies from the fully distinct species.

As an example of this phenomenon, *S. callippe macaria* and *S. c. laurina* share pale dorsal ground color, reduced basal suffusion, a pale brown to yellow disc, and a wide submarginal band on the ventral hindwing. The two subspecies differ in that *S. c. macaria* populations usually have silver spots at a frequency of 90% or more, while *S. c. laurina* populations have unsilvered spots at a frequency of 60% or more. Sette (1962) has outlined the gradual clines between these populations in the frequencies of this silvering character. Likewise, the subspecies *S. c. elaine* (silvered) differs from the subspecies *S. c. rupestris* (unsilvered) in exactly the same way. However, the *elaine-rupestris* subspecies differ from the *macaria-laurina* subspecies by combining the silvering characters with extremely dark ground color, melanic basal suffusion, a dark brown disc, and a narrow submarginal band.

It is generally agreed that populations along gradual clines should not be recognized as discrete subspecies, but populations at points along a sharp stepcline may warrant recognition. As an example, one may arbitrarily define populations as *S. c. macaria* if the frequency of silver spots is 60% or more, or as *S. c. laurina* if unsilvered in similar frequencies. Thus, populations in the Tehachapi Mountains may be called *S. c. macaria*, populations on the west slope of the Greenhorn Mountains may be called *S. c. laurina*, and populations in the Piute Mountains may be called *S. c. macaria-laurina* intergrades.

Because most independent characters vary discordantly and along gradual clines, and because most populations are not homogeneous as a result, Arnold and many others have argued that subspecies are merely arbitrary categories that have no real meaning or significance. Instead, these authors suggest that the proper way to look at geographic variation is to examine the distribution patterns of single genes or character state

frequencies, and attempt to correlate these patterns with environmental variables. While this approach is certainly of value, it does not substitute for the subspecies concept. Individual genes or character states do not exist completely detached in time and space, but belong to populations which occupy discrete geographic distributions. Moreover, it is the population that adapts to a particular set of local environmental conditions, and is the basic evolutionary unit as discussed by Ehrlich and Murphy (1981) for *Euphydryas*. Individual genes or characters are certainly not evolutionary units. In addition, geographic subspecies are the immediate precursors of full species, and are of prime importance to the basic process of allopatric speciation. The fact that most subspecies are not clearly homogeneous or sharply delimited does not alter their evolutionary importance.

With regard to the taxonomic nomenclature of subspecies, many objections have been raised to the Latin trinomen, and Arnold suggests that this classification should be largely abolished because trinominal systems "distort the real nature of character variation and bias subsequent analysis". However, it is not sufficient to consider individual genes or characters as mere abstractions completely isolated from actual populations. It is necessary to recognize populations as evolutionary units distributed in time and space, and some type of nomenclature is also necessary to recognize and discuss those populations that exhibit significant evolutionary divergence. Wilson and Brown (1953) agree with this to some extent, but suggest that the trinominal names of subspecies should be discarded in favor of vernacular names such as the "Pine Mountain Silverspot" or the "Grass Valley Silverspot". Of course the problems of ambiguity and confusion with vernacular names when applied to scientific nomenclature are well known (see Murphy & Ehrlich, 1983; Pyle, 1984). In addition, the trinominal system has a long, historical establishment in the literature, and is widely familiar to most students of the various taxonomic groups. To completely replace an established classification with an entirely new system would be extremely confusing, and is entirely unwarranted.

Perhaps the most serious concern with Arnold's classification of *Speyeria callippe* is his perception of "significant difference". He frequently refers in his paper to the differences between subspecies as "slight", "minor", and "minute". In his discriminant analysis, he was only able to correctly identify 43.2% of individuals of unknown subspecific identity. Of course, part of this problem is due to the heterogeneous overlap between subspecies along clines. However, fundamental problems in the perception of actual character differences are evident in his study. The characters used to distinguish subspecies are the same characters used to distinguish fully distinct species of *Speyeria*. Indeed, the differences in wing color pattern between subspecies are often

far greater than between full species throughout their ranges!

For example, *S. callippe callippe* differs from *S. callippe inornata* by five different characters of wing color pattern. In sharp contrast, sympatric *S. atlantis dodgei* (Gunder) and *S. hydaspe* (Bdv.) only differ consistently by one color character, and even this character often requires close examination by the human observer for correct identification. There are dozens of similar examples where the differences between subspecies are far greater than between full species. Indeed, only three species of *Speyeria* exhibit constantly diagnostic wing pattern characters, namely *S. diana* (Cramer), *S. idalia* (Drury), and *S. nokomis* (Edwards). None of the other species have completely exclusive, diagnostic wing characters that do not overlap with other species in parts of their respective ranges. Thus, *S. zerene bremnerii* (Edwards) of the Pacific Northwest is extremely similar to *S. atlantis nikias* (Ehrmann) of the southern Rocky Mountains, and many specimens can only be distinguished on the basis of geography alone. Yet sympatric populations of *S. atlantis* and *S. zerene* are usually highly divergent and easily identified. If Arnold can not distinguish *Speyeria* subspecies because the differences are too "slight" or "minor", he will have exactly the same problems distinguishing between full species.

It is useful to look at Arnold's perception problems in more detail by re-examining several of the populations used in his study. As previously discussed, the typical San Francisco *S. callippe callippe* is one of the most divergent subspecies seen within the entire species. The only similar subspecies is the more inland and southerly *S. c. comstocki*. Arnold has concluded that these subspecies can not be distinguished. While they are certainly heterogeneous with some degree of overlap in characters, these subspecies exhibit significant divergence in three color pattern characters, and they also differ significantly in average forewing length as well.

First, typical *S. c. callippe* has extremely intense melanic suffusion on the dorsal wing surfaces, while the suffusion is more reduced in *S. c. comstocki*. The suffusion in *S. c. callippe* extends to the distal parts of the wings, combined with heavy dark scaling that extends out along the veins. As a consequence, the pale dorsal median areas that correspond to the silver median spots on the ventral hindwing contrast sharply with the distal ground color. Most specimens of *S. c. comstocki* do not exhibit this sharp contrast.

The second character is the yellow overscaling on the brown disc of the ventral hindwing. Many specimens of *S. c. callippe* retain solid brown areas on the disc that are free of this yellow suffusion, particularly in the costal and limbal areas of the disc. Most specimens of *S. c. comstocki* exhibit yellow suffusion over nearly the entire disc.

The third character is the reddish ground color that covers the basal



region of the ventral forewing. In males of *S. c. callippe*, this red color extends beyond the discal cell out into cells Cu 1 and Cu 2 almost to the black median bars or even beyond. In the males of *S. c. comstocki*, this red color is largely restricted to the discal cell itself.

For the above analysis, 45 males of *S. c. callippe* from San Bruno Mountain in San Mateo County were compared with 52 males of *S. c. comstocki* from three sites in the Diablo Range. These localities are 20 miles south of Livermore in Alameda County, near Milpitas in Santa Clara County, and Del Puerto Canyon in Stanislaus County. The results are shown in Table 1. Although some degree of overlap exists between *S. c. callippe* and *S. c. comstocki* for all characters studied, this overlap is very minimal with respect to the dorsal melanic suffusion and the ventral red coloration of the male forewing. Regarding the disc colors, the frequency of light and dark color is about equal in the *S. c. callippe* sample, but the frequency of dark color is significantly reduced in the *S. c. comstocki* sample ( $\chi^2$   $p < .0001$ ). The range of *S. c. comstocki* forewing lengths is 24-29 mm with the majority of specimens falling in the 26-27 mm classes. By contrast, the range of *S. c. callippe* forewing lengths is 28-32 mm with the majority of specimens falling in the 29-30 mm classes. While no single character trait is exclusively confined to either subspecies, the general pattern of character frequencies is one of very strong divergence between the *S. c. callippe* and *S. c. comstocki* subspecies.

Therefore, it is concluded that Arnold's study has failed to perceive the major differences that actually exist among the diverse subspecies of *Speyeria callippe*. Significant divergence between geographically contiguous subspecies such as typical *S. c. callippe* and *S. c. comstocki* is a tangible reality, despite some degree of heterogeneous overlap between such populations. More remotely spaced subspecies such as *S. c. comstocki* and *S. c. rupestris* exhibit a far greater degree of evolutionary divergence as one might expect. At the most extreme level of divergence, as between *S. c. rupestris* and *S. c. harmonia*, one would never suspect that such taxa belonged to the same species or were even remotely related. The conspecific relationships of such extremes are only known because of the existence of intergrading populations along gradual clines. Early authors had quite valid reasons to believe that such taxa were fully distinct species when they were first described. The subsequent discovery of intermediate clinal populations does not mean that this evolutionary diversity and adaptive radiation within *S. callippe* no longer exists or is not a reality. Divergent populations require recognition and some type of taxonomic nomenclature for discussion purposes. Merely describing the distribution frequencies of individual genes or character traits detached from actual populations is completely inadequate.

Subspecies represent significant levels of evolutionary divergence, often nearly as much as full species. The heterogeneous overlap between

contiguous subspecies or the discordant variation of independent character traits does not reduce this significance. Thus, it is suggested that the historical subspecies classification of *S. callippe* and other species of *Speyeria* should be retained, because such a classification serves to recognize important evolutionary phenomena.

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Table 1. Frequencies of dorsal melanic suffusion, ventral red color, and disc color in samples of *Speyeria callippe callippe* and *S. c. comstocki*.

	intense suffusion	light suffusion	intense red	reduced red	dark disc	light disc
<i>callippe</i> (n=45)	.93	.07	.93	.07	.49	.51
<i>comstocki</i> (n=52)	.10	.90	.15	.85	.15	.85

*Appendix I.* The following outline lists the characteristics and distribution of each *Speyeria callippe* subspecies. As noted by Arnold, the geographic variation of this species segregates into three major subspecies groups as defined below. However, significant variation also exists in each of these groups, particularly the Californian *callippe* group. One taxon, *S. callippe gallatini* (McDunnough), does not appear to have any distinguishing characteristics that separate it from *S. c. calgariana*, and is probably best regarded as a synonym of this latter taxon. Also, *S. c. sierra* must be regarded as a synonym of *S. c. juba* as previously discussed.

1. *callippe* group — dorsal forewing with thick, dark veins in male, ventral hindwing with dark brown to yellow disc, spots silver or unsilvered, median spots pointed or rounded but not large and elongate, distinct yellow submarginal band.
2. *semivirida* group — dorsal forewing with thin, light veins in male, ventral hindwing with greenish brown to brown disc, spots always silver, median spots very large and elongate, yellow submarginal band present or absent.
3. *nevadensis* group — dorsal forewing with thin, light veins in male, ventral hindwing with green to gray disc, spots always silver, median spots very large and elongate, yellow submarginal band present or absent.
- 1a. *S. callippe callippe* (Bdv.) — dorsal wings with pale yellow-orange ground color combined with very extensive basal suffusion, ventral forewing with extensive reddish color in male, ventral hindwing with a brown disc covered with yellow suffusion, spots always silver, median spots pointed, narrow submarginal band.  
Distribution — San Francisco Bay area.
- 1b. *S. callippe comstocki* (Gunder) — differs from typical *callippe* in having reduced basal suffusion on dorsal wings, mostly yellow color on ventral forewing of males, and a mostly yellow disc.  
Distribution — inland and southern Coast Range from Contra Costa Co. to Baja California.
- 1c. *S. callippe macaria* (Edwards) — dorsal wings medium orange with almost no basal suffusion, ventral forewing of male with extensive reddish color, ventral hindwing with pale brown to yellow disc, spots usually silver (90% or more), median spots small and pointed, submarginal band very wide covering nearly a third of the hindwing.  
Distribution — Tehachapi Mts., Ventura Co. to Kern Co.
- 1d. *S. callippe laurina* (Wright) — differs from *macaria* only in having a high frequency of unsilvered spots (60% or more).  
Distribution — west slope Greenhorn Mts., Kern Co. to southern Tulare Co.
- 1e. *S. callippe inornata* (Edwards) — dorsal wings medium to ruddy orange with moderate basal suffusion, ventral hindwing with a light to dark, dull brown disc, spots usually unsilvered, median spots large, round to pointed, submarginal band narrow.  
Distribution — low foothills along Sierra Nevada west slope, Shasta Co. to northern Tulare Co.
- 1f. *S. callippe juba* (Bdv.) west slope race ("*laura*" phenotype) — differs from



*inornata* in having silver spots and a wide yellow submarginal band. Disc color light to dark brown.

Distribution — high elevations along the Sierra Nevada west slope, Tehama Co. to Placer Co.

- 1g. *S. callippe juba* east slope race (“sierra” phenotype) — differs from the west slope race in having almost no basal suffusion on the dorsal wings, a very pale brown or yellow disc, often with a greenish tinge, and in having very small wing size (male forewing length usually 26-27 mm).

Distribution — high elevations along the Sierra Nevada east slope, Lassen Co. to Eldorado Co.

- 1h. *S. callippe rupestris* (Behr) — differs from *inornata* in having dark ruddy orange ground color combined with very extensive basal suffusion on the dorsal wings. Ventral hindwing with a dark red-brown to dull brown disc, spots usually unsilvered (80% or more).

Distribution — northern Coast Range and Salmon-Trinity Mts., Mendocino Co. to Siskiyou Co.

- 1i. *S. callippe liliana* (H. Edwards) — differs from *rupestris* and typical *callippe* in having only light basal suffusion; differs from typical *callippe* in having ruddy orange dorsal ground color, and a solid red-brown disc without much yellow suffusion; differs from *rupestris* in having silver spots.

Distribution — California Coast Range, Napa Co. to Glenn Co.

- 1j. *S. callippe elaine* dos Passos & Grey — differs from *rupestris* in having a high frequency of silver spots (80% or more). Populations from Mt. Shasta to the Oregon Siskiyou Mts. have a dark red-brown to dull brown disc. Populations from the Oregon Cascade Range (west slope) have a dark slate-brown to jet black disc, often with greenish suffusion from Douglas Co. to Linn Co.

Distribution — northern Siskiyou Co. California to Linn Co. Oregon.

- 2a. *S. callippe semivirida* (McDunnough) — dorsal wings pale yellow orange with thin veins in male, ventral hindwing with a light to dark disc, greenish brown to slate-brown, silver median spots very large and elongate, yellow submarginal band narrow or obliterated with brown suffusion.

Distribution — east slope of the Cascade Range from Klamath Co. Oregon to British Columbia, east through northern Idaho.

- 2b. *S. callippe semivirida* “Columbia” race — differs from typical *semivirida* in having dark orange ground color on dorsal wings, and a dark red-brown to “chocolate” brown disc on ventral hindwing.

Distribution — south-central British Columbia.

- 3a. *S. callippe nevadensis* (Edwards) — differs from *semivirida* in having a pale yellow-green disc and a distinct yellow submarginal band.

Distribution — foothills along Sierra Nevada east slope, eastern California from Lassen Co. to Inyo Co. east to western Nevada.

- 3b. *S. callippe harmonia* dos Passos & Grey — differs from *nevadensis* in having the submarginal band obliterated with green suffusion. Disc color yellow-green, bright green, or gray-green.

Distribution — eastern Nevada, Utah, Idaho, western Colorado to western Montana.

- 3c. *S. callippe meadii* (Edwards) — differs from *harmonia* in having considerable dark basal suffusion on the dorsal wings, disc color bright green to dark

olive-green.

Distribution — Colorado Front Ranges east of Continental Divide.

- 3d. *S. callippe calgariana* (McDunnough) — differs from *harmonia* in having a high frequency of gray and gray-green discs, bright green or yellow-green colors usually scarce or absent.

Distribution — east of Continental Divide, Canadian prairies of Alberta to Manitoba, south to eastern Wyoming and western Nebraska.